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The Breeding Biology of the Male Brown Bear *(Ursus arctos)*[1,2]

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(Plates I-IX; Text-figures 1-2)

Introduction

THE BREEDING BIOLOGY of the brown bear is known in only a general way. Breeding occurs in the spring, usually in late May or June, and its timing does not appear to vary significantly between wild or captive animals or throughout the wide expanse of the species distribution (Dathe, '61; Dittrich and Einsiedel, '61; DeVoto, '53; and Murie, '44). The female exhibits a period of heat extending up to two weeks and is polygamous. During this time coital activity is recurrent but is interrupted by days of nonbreeding (Dittrich and Kronberger, '63).

The age of puberty is unknown in the male bear, but among female captives is usually attained at three and a half years. The gestation period in captivity has been reported as varying between 194 and 278 days (Dittrich and Kronberger, '63). Despite this disparity, a large body of evidence shows whelping to occur regularly in late January and early February regardless of when breeding occurs. Explanation for this is that bears of the genus *Ursus* have a delayed implantation wherein the fertilized eggs develop to the blastocyst stage and lie quiescent in the uteri for a long period of time. Implantation occurs about the same time in all specimens regardless of when breeding occurs (Wimsatt, '63; and Dittrich and Kronberger, '63). Normally the delays last slightly over half of the gestation period and macroscopic embryos are not visible until about the time of winter denning. The cubs are born in an immature state during the so-called hibernation period. Litters vary from one to four cubs but are usually two or three.

Beyond breeding observations, the only specific information known to us on the reproductive biology of the male bear is a report by Dittrich and Kronberger ('63) on the histology of the testes and epididymides of two captive bears killed in August and October, respectively. On the basis of spermatogenic activity and epididymal sperm observed in both animals, they concluded that male brown bears retain reproductive capability at least through October.

Methods and Procedures

The testes, epididymides, and vasa deferentia of 127 brown bears were collected in Alaska between May 20, 1961, and November 11, 1964. The majority of the specimens were from Kodiak Island, but specimens were obtained also from other areas of the state, particularly from the Alaska Peninsula (Table I). Most of the bears were killed by sport hunters. Additional specimens were obtained from bears killed as nuisances or by unilateral castrations of live-trapped bears.

[1]Reference to the brown bear here refers collectively to the various so-called species of North American brown and grizzly bears, and to the European and Eurasian brown bears. Recent taxonomic reviews conclude that all of these are simply subforms of *Ursus arctos* L. (Pocock, '32; Erdbrink, '53; Couturier, '54; and Rausch, '62).

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TABLE I RESULTS OF EXAMINATIONS OF TESTES, EPIDIDYMIDES,

Location	*Specimen Number*	*Date*	*Skull*[1] *Meas.*	*Age*[2] *(Years)*	*Testis*[3] *Wt. (Gms.)*	*Testis Tubules* Diam. (μ)	*Testis Tubules* Activity[4] State
Kodiak Is.	14N	4-7-64	19¼	1.2e	9.7*	.....	NF, G
	36M	5-4-62	.....		18.2	95	NF, G
	12M	5-7-62	19⅝	2.3e	17.2	113	NF, G
	8N	5-8-64	20⅜	2.3a	11.8	.....	NF, G
	47M	5-11-63	22½	2.3e	15.0*	.....	NF, G
	49M	5-13-62	21½	2.3e	19.0*	.....	NF, G
	5M	5-14-62	.....		24.0	112	NF, G
	57M	5-19-63	19½	1.3e	11.0	.....	NF, G
	26M	5-19-62	20½	2.3e	19.4	95	NF, G
	43N	5-19-64	21¼	2.3e	16.7*	.....	NF, G
	K44	5-20-62	.....	2.3a	6.3*	86	NF, G
	65M	5-21-63	19⅞	1.3e	10.0*	.....	NF, G
Anchorage	E306	7-14-63	.....		11.0*	83	NF, G
Kodiak Is.	40N	10-7-64	.....		15.0*	81	NF, G
	49N	10-7-64	.....		10.2*	.....	NF, G
	71M	10-8-63	21⅛	2.7e	10.2*	.....	NF, G
	2M	10-10-62	20⅝	2.7e	16.0	75	NF, G
	3M	10-10-62	20⅝	2.7e	13.9	94	NF, G
	31A	10-11-61	23$^{3}/_{16}$	2.7a	20.1	.....	NF, G
	4M	10-12-62	.....		21.9	118	NF, G
	67A	10-12-63	20$^{13}/_{16}$		11.7	81	NF, G
	32A	10-17-61	23$^{1}/_{16}$	2.8a	19.2	.....	NF, G
	K97	10-17-63	21¼	2.8a	16.5*	.....	NF, G
	34MK	10-19-61	.....		22.9	.....	NF, G
	75M	10-19-63	.....		24.2*	.....	NF, G
	47N	10-22-64	20	2.8e	23.1*	109	NF, G
	20M	10-25-62	.....		15.8	123	NF, G
	52N	10-29-64	.....	2.8e	20.8*	97	NF, G
	18M	10-31-62	21⅛	2.9e	16.3	114	NF, G
	46N	11-2-64	19.0	1.9e	6.5*	54	NF, G
	50N	11-2-64	23½	2.8k	15.8*	.....	NF, G
	51N	11-3-64	20	2.9e	13.2*	96	NF, G
	8M	11-5-62	22½	2.9e	22.1	.....	NF, G
	10M	11-8-62	20⅞	2.9e	15.1	.....	NF, G

[a] For explanation of number designations see Table II.

TABLE II RESULTS OF EXAMINATIONS OF TESTES, EPIDIDYMIDES,

Location	*Specimen Number*	*Date*	*Skull*[1] *Meas.*	*Age*[2] *Yrs.: Months*	*Testis*[3] *Wt. (Gms.)*	*Testis Tubules* Diam. (μ)	*Testis Tubules* Height of Epithel (μ)	*Testis Tubules* Activity[4] State
Kodiak Is.	36N	5-7-64	.....		42.5*	.....	.....	SN
	59M	5-11-63	.....		36.0*	.....	.....	S, G
	13N	5-18-64	21⅞	3.3e	33.4	124	.....	NF, G
	21M	5-22-62	22	3.3e	25.6	196	35	SN
	56M	5-24-63	.....		43.0*	173	39	FS, A
	E042	5-25-61	.....		24.5 30.8	187	.....	S, G
Paxson	E258	9-16-62	.....		20.0 18.8	123	32	NF, G
Kodiak Is.	62A	10-4-62	22$^{7}/_{16}$	3.9e	31.9*	154	51	SN, G
	32N	10-5-64	22$^{15}/_{16}$	3.9e	46.0	.....	.....	A, FS
	30N	10-7-64	24⅛	4.9e	34.6*	.....	.....	SN, G
	72M	10-9-63	24	4.9e	27.3	.....	.....	NF, G
	9M	10-10-62	.....		33.9	180	38	SN, G
	73M	10-14-63	.....		29.1	125	57	S, G
	74M	10-17-63	25¼	4.9e	21.4	.....	.....	NF, G

Legend for Tables I, II, III

[1] Skull measurements: Length (occipital protuberance to margin of incisor) + width (outer edges of zygomatic arches).

[2] Age: k = known age marked animal; a = approximate known age marked animal; e = estimated age.

[3] Testis weight: testis + epididymis + vas deferens. The weights marked with an asterisk are preserved weights plus 10% (the mean weight loss between fresh and preserved specimens).

[4] Spermatogenic activity: FS = free sperm; SN = sperm nuclei or heads in Sertoli cells; S = primary or secondary spermatocytes; A = abnormal forms shed into lumen; G = Edematous (giant) cells in germinal epithelium or in lumen. NF = No formed elements other than giant cells.

AND VASA DEFERENTIA OF INFANTILE BROWN BEARS[a]

Intertubular Area			*Epididymis*					*Vas Deferens*		
General[5] Character	Cytoplasmic Abundance[6]	Vacuolation[7]	Diam. (μ)	Height of Epithel (μ)	Lumen[8] Contents	Coagulum[9]	Cytoplasmic[10] Droplets	Lumen[8] Contents	Coagulum[9]	Cytoplasmic[10] Droplets
FI	.....	.....	.....	.....	E	.....	+++	E	++	+++
IF	+	A, H	178	48	E	+	+	E	N	+
IF	+	A, H	196	50	E	+	+	E	++	++
FI	+	A, H	150	47	E	+++	+	E	++	++
FI	+	A, H	.....	.....	E	+	++	E	+	++
IF	+	A, H	.....	.....	E	+	+	E	+	+
IF	++	A, H	271	62	E	++	++	E	+	++
FI	+	N	.....	.....	....	.....	.....	....	.....	.....
FI	+	A, H	123	36	E	+++	N	E	.....	.....
FI	+	A, H	.....	.....	E	+	+	E	+	++
FI	+	N	169	60	E	++	+	E	.....	.....
FI	+	N	.....	.....	E	.....	.....	E	.....	.....
FI	+	A, H	.....	.....	E	N	+	E	.....	.....
FI	+	A, H	176	51	E	N	N	E	N	N
FI	+	N	.....	.....	E	.....	.....	E	.....	.....
FI	+	N	.....	.....	E	.....	.....	E	.....	.....
I	+	A, H	180	46	E	+	N	....	.....	.....
FI	+	N	194	57	E	+	+	E	N	+
FI	+	A, H	.....	.....	E	N	N	E	++	++
IF	+	A, H	205	51	E	N	N	E	N	+
IF	+	A, H	206	.....	E	++	N	E	+	N
IF	++	A, H	.....	.....	E	.....	.....	E	.....	.....
IF	++	A, H	.....	.....	E	.....	.....	E	.....	.....
IF	+	A, H	.....	.....	E	.....	.....	E	.....	.....
....	.....	.....	.....	.....	....	.....	.....	....	.....	.....
FI	+	A, H	159	55	E, A	+	+	....	.....	.....
IF	+	A, H	215	.....	E	++	+	E, D	N	N
IF	+	A, H	122	33	A	+++	+	....	.....	.....
FI	+	A, H	173	37	E	N	+	E	N	+
FI	++	A, H	150	35	E	++	+	....	.....	.....
IF	+	A, H	.....	.....	E	+	+	E	N	N
IF	+	A, H	206	.....	E	++	N	E	++	N
FI	+	A, H	.....	.....	E, D	N	+	....	.....	.....
FI	+	A, H	.....	.....	E, D	N	N	....	.....	.....

AND VASA DEFERENTIA OF PREPUBERAL BROWN BEARS

Intertubular Area			*Epididymis*					*Vas Deferens*		
General[5] Character	Cytoplasmic Abundance[6]	Vacuolation[7]	Diam. (μ)	Height of Epithel (μ)	Lumen[8] Contents	Coagulum[9]	Cytoplasmic[10] Droplets	Lumen[8] Contents	Coagulum[9]	Cytoplasmic[10] Droplets
.....	.....	.....	.....	.....	E	.....	.....	E	.....	.....
I	+	A, H	.....	.....	A, S	+++	+	E, A, S	+	++
IF	+	A, H	.....	.....	E, A	++	N	E	++	+
FI	+	A, H	182	45	A	+	N	A	+	++
I	++	A, H	224	68	S, A	+++	++	S, A	++	N
IF	+	A, H	194	.....	A	.....	.....	.....	.....	.....
FI	+	A, H	.....	.....	.....	.....	.....	.....	.....	.....
IF	+	A, H	224	57	E	+	+	E	N	+
IF	+	A, H	.....	.....	A, S	.....	.....	A, S	N	N
FI	+	L	159	47	A	+	+	A	N	+
IF	+	A, H	.....	.....	E	.....	.....	E	.....	.....
FI	+	L	248	66	E, A	++	+	E, A	+	N
IF	++	A, H	167	.....	E	+	++	E, D	N	N
IF	.....	A, H	.....	.....	.....	.....	.....	.....	.....	.....

[5] General character of intertubular tissue: FI = more fibrous tissue than interstitial tissue; IF = more interstitial tissue than fibrous tissue; I = predominantly interstitial tissue.

[6] Leydig cell cytoplasmic abundance: + = low; ++ = med.; +++ = high.

[7] Leydig cell vacuolation: N = little or none; A = abundant small vacuoles; L = large and small vacuoles; H = vacuoles highly vesicular (frothy).

[8] Lumen contents: S = apparently viable sperm; A = immature and abnormal forms; D = degradation products of tract; E = empty; several entries indicate differences between ducts in order of decreasing occurrence.

[9] Prevalence of coagulum in epididymis and vas deferens: N = little or none; + = low; ++ = medium; +++ = abundant.

[10] Cytoplasmic extrusions of epididymis and vas deferens: N = little or none; + = low; ++ = medium; +++ = abundant.

TABLE III RESULTS OF EXAMINATIONS OF TESTES, EPIDIDYMIDES,

Location	*Specimen Number*	*Date*	*Skull*[1] *Meas.*	*Testis*[3] *Wt. (Gms.)*		*Testis Tubules* Diam. (μ)	Height of Epithel (μ)	Activity[4] State
Kodiak Is.	41M	4-2-63	29	94*		285	95	FS
	42M	4-18-63	26¾	83*		271	solid	FS
	22M	4-22-62	23⅜	49		187	solid	FS
	42N	4-28-64	25⅜	58*		.....	.....	FS
	34N	5-1-64	.....	60*		.....	.....	FS
	44M	5-2-63	.....	90*		.....	.....	FS
	16M	5-4-62	28½	98		276	76	FS
	45M	5-4-63	28½	47*		.....	.....	FS
	1M	5-4-62	28⅜	95		262	95	FS
	33N	5-5-64	28 3/16	85*		.....	.....	FS
	43M	5-5-63	28½	84*		.....	.....	FS
	31N	5-6-64	27½	110*		.....	.....	FS
	13M	5-7-62	26¾	77		209	57	FS
	31M	5-8-62	.....	89		257	76	FS
	46M	5-9-63	26½	46*		.....	.....	FS
	28M	5-10-63	.....	79		.....	.....	FS
	33M	5-10-62	27¾	97		259	83	FS
Alaska Pen.	E231	5-10-62	.....	72	74	.....	.....	FS, A
Kodiak Is.	61M	5-11-63	28½	86*		.....	.....	FS
Alaska Pen.	E305	5-11-64	.....	92	90	.....	.....	FS, A
	1396	5-12-64		76*	80*	266	59	FS
Kodiak Is.	7M	5-13-62	.....	76		268	76	FS, A
	15M	5-14-62	27	70		218	83	FS
	6M	5-15-62	29	100		228	66	FS
	40M	5-15-62	27⅞	94		218	66	FS
	48M	5-15-63	28½	77		.....	.....	FS
	53M	5-15-63	28	121*		237	83	FS
	9N	5-16-64	.....	71*		.....	.....	FS
	11M	5-16-62	.....	67		.....	.....	FS
	14M	5-16-62	29¼	56		228	66	FS
Alaska Pen.	3093	5-16-64	.....	52*		.....	.....	FS
Kodiak Is.	54M	5-16-63	27	65*		.....	.....	FS
Alaska Pen.	3094	5-16-64	.....	45*		.....	.....	FS
Kodiak Is.	24M	5-17-62	22½	73		200	47	FS
	34M	5-17-62	28¾	91		180	59	FS
	3N	5-18-64	28⅛	111		.....	.....	FS
	55M	5-18-63	26½	48*		.....	.....	FS
Alaska Pen.	3099	5-18-64	.....	70*		.....	.....	FS

AND VASA DEFERENTIA OF SEXUALLY MATURE BROWN BEARS[a]

Intertubular Area			*Epididymis*					*Vas Deferens*		
General[5] Character	Cytoplasmic Abundance[6]	Vacuolation[7]	Diam. (μ)	Height of Epithel (μ)	Lumen[8] Contents	Coagulum[9] Prevalence	Cytoplasmic[10] Droplets	Lumen[8] Contents	Coagulum[9]	Cytoplasmic[10] Droplets
I	+++	L	268	64	S	N	+	S, A	N	+
I	+++	L	262	67	S, E	+	+	S	+	+
IF	+	N	253	62	S, A, E	+	++	A, S	+	N
I	++	L	.....	.....	S, A	+++	+	.....	.....	.....
I	+++	L	.....	.....	S	.....	.....	S	.....	.....
I	++	A	.....	.....	S	.....	.....	S	.....	.....
I	+++	L	279	70	S	N	+	S	N	+
IF	+	A	.....	.....	S	.....	.....	S	+	++
I	++	A	271	66	S, A, E	N	+++	S, A	N	+
I	++	A	.....	.....	S	N	+	S	N	N
I	+++	A	.....	.....	S	N	+	.....	.....	.....
IF	+	A	.....	.....	S	.....	.....	S	.....	.....
I	+++	L, H	275	63	S	N	+	S	N	N
I	++	L	307	59	S, A	N	+++	S	N	+
I	+++	L	.....	.....	S	N	++	S	+	++
I	+++	L, H	.....	.....	S	N	++	S	N	+
I	+++	L, H	319	47	S, E	N	++	S	N	+
I	++	L, H	.....	.....	S	+	++	.....	.....	.....
I	+++	L, H	.....	.....	S	+	++	S	N	+
I	+++	L, H	317	64	S, A	++	+++	S, A	N	+
I	+++	L, H	326	66	S, A	N	+	S, D	N	++
I	+++	L, H	323	80	S, A	N	+++	S, A	N	+++
I	+++	L, H	262	49	S, A	N	++	S, A	N	++
I	+++	A, H	279	59	S, A	+	+++	S, A	+	N
I	++	L, H	360	64	S	+	++	S, D, A	N	N
I	+++	L	.....	.....	S	N	N	S	+	N
I	++	A, H	342	71	S, A	+	+++	S, A	+	++
I	+++	L	.....	.....	S	N	+	S	+	+
I	++	A, H	234	59	S	+	++	S	N	+
IF	+	A, H	224	53	S, A, E	+	+	S, A	N	+
I	++	L, H	.....	.....	S	++	+	S	.....	.....
I	+++	L	.....	.....	S	N	N	S	N	+
I	++	A, H	243	59	S	+	+	.....	.....	.....
I	+	A, H	234	63	E, S	++	++	E, S	N	++
I	+++	L	317	51	S, E	+++	N	S	N	N
I	+++	L, H	.....	.....	S	+	N	S	N	N
I	+++	A, H	.....	.....	S	+	+	S	N	N
I	+++	A, H	.....	.....	S	N	N	S	N	N

Table III continued on next page.

TABLE III (continued) RESULTS OF EXAMINATIONS OF TESTES, EPIDIDYMIDES,

Location	*Specimen Number*	*Date*	*Skull*[1] *Meas.*	*Testis*[3] *Wt. (Gms.)*	*Testis Tubules* Diam. (μ)	Height of Epithel (μ)	Activity[4] State
Kodiak Is.	4N	5-19-64	.....	48*	.....	.....	FS
	15N	5-19-64	.....	59*	.....	.....	FS
	30M	5-19-62	25½	78	265	76	FS
	41N	5-19-64	.....	73	.....	.....	FS
	51M	5-19-63	26¼	92*	247	66	FS
	64M	5-19-63	27¾	.....	.....	.....	FS
	27M	5-20-62	24⅞	64	216	59	FS
	23M	5-22-62	27⅛	97	218	58	FS
	50M	5-22-63	27½	80*	266	82	FS
	52M	5-22-63	29¼	113*	264	83	FS
	17M	5-23-62	26¼	70	230	66	FS
	35M	5-23-62	28⅞	89	269	67	FS
	58M	5-23-63	.....	69*	253	65	FS
	32M	5-24-62	28½	78	246	76	FS
	37M	5-24-62	28½	87	263	75	FS
	38M	5-24-62	28⅜	86	243	.....	FS
	19M	5-25-62	27¾	83	294	77	FS, A
	39K	5-25-63	.....	87*	.....	.....	FS
	63M	5-25-63	27¾	52*	.....	.....	FS
	39M	5-28-62	28	85	.....	.....	FS
	29M	5-29-62	27	96	285	83	FS
	68M	5-30-63	26½	.....	.....	.....	FS
	62M	5-31-63	27½	.....	.....	.....	FS
Alaska Pen.	E252	5-?-63	.....	.....	.....	.....	FS
Kodiak Is.	60M	6-1-63	.....	52*	.....	.....	FS
	66M	6-12-63	.....	84*	.....	.....	FS
Alaska Pen.	1812	7-14-63	.....	52*	253	77	FS
	1820	7-17-63	.....	84*	276	76	FS
	1825	7-18-63	.....	68*	247	76	FS
	1827	7-19-63	.....	78*	237	59	FS, A
	1831	7-21-63	.....	52*	209	60	FS, A
Kodiak Is.	78M	8-3-63	.....	53*	206	66	A, FS
	69M	10-1-63	25¼	.....	.....	.....	FS, A
	70M	10-2-63	26⅜	.....	.....	.....	FS
	42A	10-17-62	22 15/16	54*	184	44	FS, A
	48N	11-4-64	22¼	55*	.....	.....	FS, A
	55N	11-10-64	28¼	81*	199	47	SN, A
Kodiak Is.	54N	11-10-64	28⅛	56*	169	53	SN, A

[a] For explanation of number designations see Table II.

AND VASA DEFERENTIA OF SEXUALLY MATURE BROWN BEARS[a]

Intertubular Area			*Epididymis*					*Vas Deferens*		
General[5] Character	Cytoplasmic Abundance[6]	Cytoplasmic Vacuolation[7]	Diam. (μ)	Height of Epithel (μ)	Lumen[8] Contents	Coagulum[9] Prevalence	Cytoplasmic[10] Droplets	Lumen[8] Contents	Coagulum[9]	Cytoplasmic[10] Droplets
IF	++	A, H	.....	.....	S	N	N	S	N	N
I	+++	L, H	.....	.....	S	N	N	S	N	N
I	+++	A, H	267	52	S, A	N	+	S	N	+
IF	++	A, H	.....	.....	S	N	+	S	N	N
I	+++	L, H	293	63	S, E	N	+	S	N	+
I	++	A, H	.....	.....	S	N	N	S	N	N
I	++	A, H	253	59	S	+	++	S	+	+
I	+++	L, H	275	68	S	+++	+	.....	.....	.....
I	+	A, H	360	71	S	+	+	S	N	+
I	+++	L	333	56	S	++	N	S	N	N
I	+++	L	325	67	S	N	+	S	N	N
I	+++	A, H	317	63	S	+	+	S	N	+
I	++	A, H	298	64	S	N	+	.....	.....	.....
I	+++	A, H	309	71	S	N	+	S	N	N
I	++	A, H	326	71	S, E	+	+	S	N	+
I	+++	L, H	288	64	S, A	++	+	S, A	N	+
I	+++	L, H	355	74	S, A	N	N	S	N	N
I	++	A, H	.....	.....	S	+	+	S	N	+
I	+++	A, H	.....	.....	S	N	+	S	N	N
I	++	A, H	.....	.....	S, A	N	C	S	N	N
I	+++	L, H	271	62	S	N	+	S	N	+
I	++	A, H	.....	.....	S, E	.....	.....	.....	.....	.....
I	+++	L, H	.....	.....	S	N	N	S	N	N
I	++	A, H	.....	.....	S	N	N	.....	.....	.....
I	+	A, H	.....	.....	S	N	N	S, D	N	N
I	+++	L	262	62	S	N	N	S	N	N
I	++	A, H	271	63	S	N	+	S	N	N
I	+++	A, H	261	66	S	N	+	.....	.....	.....
I	++	A, H	.....	.....	S	N	+	E, S	N	+
I	++	A, H	.....	.....	S, E	N	N	E, S	N	N
I	++	A, H	253	66	S, A	+	+	S, A	N	N
IF	+	A, H	224	64	S, A, D	+	+	.....	.....	.....
....	.....	.....	.....	.....	S, A	.....	.....	.....	.....	.....
....	.....	.....	.....	.....	S	.....	.....	S	.....	.....
I	++	A, H	234	59	S, D, A	N	+	.....	.....	.....
IF	++	A, H	.....	.....	A, S	+	+	A, D, S	N	N
I	++	L	215	59	A, D, S	++	N	A, D, S	N	N
IF	++	A, H	262	39	A, S, D	++	+	E, A, D, S	N	N

The reproductive tracts of six bears were of known approximate age as established on the basis of returns from animals live-trapped and marked as cubs or yearlings (Troyer, *et al.*, '62). The remaining specimens were estimated as to sexual status on the basis of skull sizes, and testicular weight and histological comparisons with the known-age animals.

Male reproductive tracts were removed, the testes dissected free from the tunica vaginalis, and the epididymides and proximal segments of the vasa deferentia left in contact with the testes (Pl. I, figs 1-3). When possible the testes were weighed fresh; otherwise, the fixed weight was determined and adjusted to the fresh weight (Table II). The specimens were fixed in 10 percent formalin and stored in 70 percent ethyl alcohol. Histologic sections of all specimens were prepared from the body of the epididymis together with the underlying portion of the testis and the adjacent portion of the vas deferens, where available, and from other areas of the reproductive tract for representative specimens.

Sperm morphology and maturation were determined by examining sperm taken from various areas of preserved epididymides and vasa deferentia. The sperm were stained in a 1 percent solution of osmium tetroxide and the anatomical features of whole preserved sperm were then studied and measured with the light and electron microscope.

The data available for the specimens studied are listed in Tables I to III. The specimens were classed as being infantile, prepuberal, or sexually mature as determined from histological findings. Infantile specimens exhibited little or no spermatogenic activity. Prepuberal specimens showed some spermatogenesis but not to a sexually functional state. Sexually mature bears represented one of three reproductive states: (1) preseasonal—namely animals recovering from a nonbreeding period; (2) sexually active—bears in or near full breeding condition; or (3) postseasonal—animals showing spermatogenic decline following the breeding season.

Included for each specimen, if available, are the collection date, an age classification, body weight, testicular weight, the combined length plus zygomatic width of the skull, and the histologic classification of the testis, epididymis, and vas deferens (Tables I to III).

Observations

Estimates of Age and Reproductive State

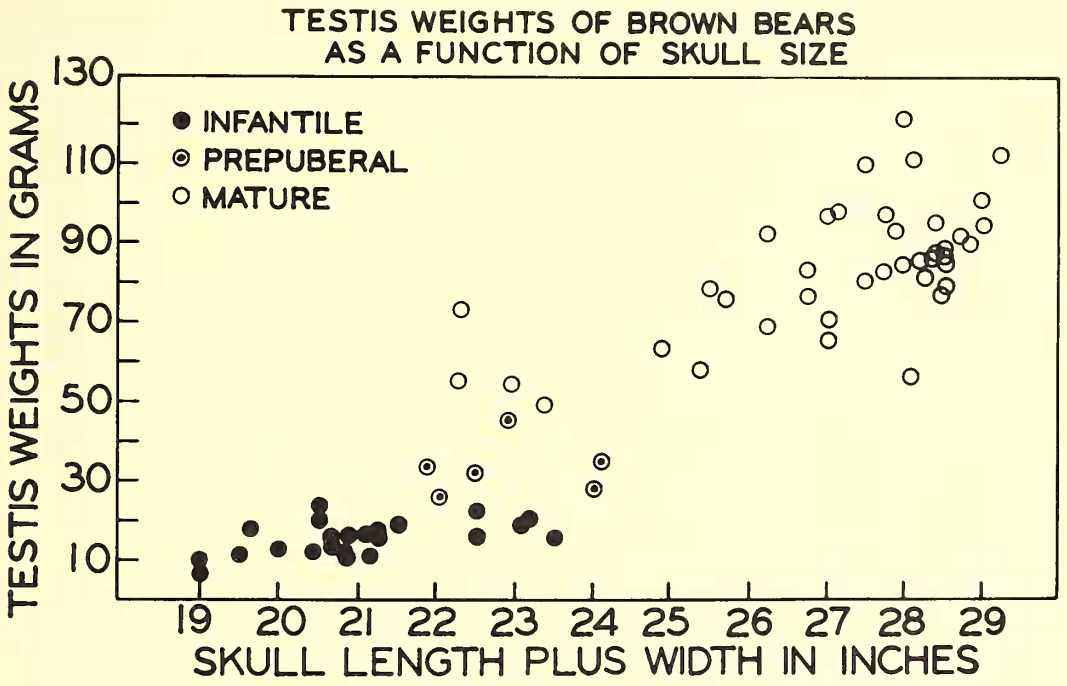
Reliable procedures for estimating the ages of bears are not available. Nonetheless the specimens included in this study were readily identified as infantile, prepuberal, or adult on the basis of testicular histology. It early became apparent, too, that skull sizes and testicular weights might also provide useful criteria for determining the reproductive maturity of bears and for estimating their approximate ages, at least in younger animals.

As seen in Text-figure 1 and Tables I to III, the size of the brown bear's testis appears to be directly correlated with the size of the skull and thus, presumably, with age. Although there are individual and seasonal variations, it will be noted that single testes of mature specimens range upward in weight from approximately 50 gms; those of infantile bears weigh approximately 25 gms or less. The limited known-age specimens available (Table I) suggested that the infantile group included bears to three years and occasionally older. The sexually mature specimens were presumably four or more years of age. The testis weights of presumed prepuberal bears based on histological examination were found to fall roughly between those of the infantile and sexually mature animals but overlapped each group slightly (Text-fig. 2 and Tables I to III). The overlap is attributed to the different ages at which individual male bears attain sexual maturity. Dittrich and Kronberger ('63) have reported similar variations in the time of sexual maturity in the female brown bear.

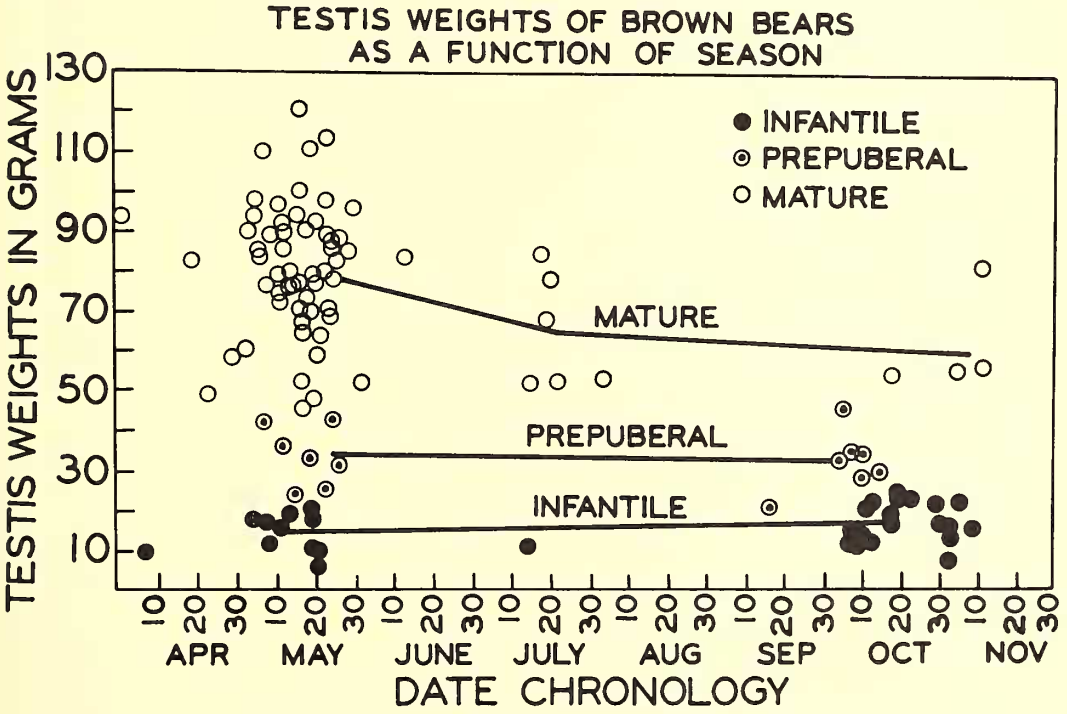
Most male bears apparently attain prepuberty in their fourth year and became sexually mature at approximately four and one half years of age. Presumably, as judged by the widely divergent skull sizes of prepubal bears a few attain this state in their third year and others not until their fifth year (Tables I to III and Text-fig. 1). The four sexually mature specimens with skulls measuring only 22 and 23 inches in length plus width and separate from the remaining mature animals, and the five infantile bears with skulls in the same size range and separate from the remaining infantile specimens, provide further evidence that the age of puberty is quite variable among male bears (Text-fig. 1).

The relative age and sexual status of bears may also be judged with fair accuracy from the skull (Tables I to III and Text-fig. 1). Animals with combined skull length and width measurements exceeding 24½ inches are quite assuredly sexually mature specimens exceeding four years of age. Conversely, specimens with skulls measuring less than 22 inches are, generally, immature. Between these limits is a group of bears of mixed sexual status, the majority presumably being prepuberal animals in their fourth year of life (Tables I to III and Text-fig. 1).

While paired testes were obtained from only a few bears, there was no indication that signi-



TEXT-FIG. 1. Testis weights of brown bears as a function of skull size.



TEXT-FIG. 2. Testis weights of brown bears as a function of season.

ficant differences existed between left and right testicular weights in the brown bear (Table III). The heaviest testis weighed 121 gms. The mean testis weight was 80 gms for the sexually mature bears, 31 gms for the prepuberal bears, and 12 gms for the infantile bears. There were, however, seasonal variations in the testicular weights of bears. Among sexually mature specimens heaviest testes occurred during the breeding season in May and June (Table III and Text-fig. 2). Testicular weights were then approximately one-third greater than during the fall postbreeding season, and conceivably at least twice as heavy as at the time of maximum testicular regression in midwinter. The decline in weight is in large measure attributable to shrinkage of the seminiferous tubules during the nonbreeding season (Table IV). A similar condition has been reported in the black bear (Erickson and Nellor, '64). In contrast to the spring to fall testicular weight decline in the adult bear, an opposite condition occurs in the infantile bear. Here, fall testicular weights exceed spring weights presumably because the infantile bear realizes substantial body growth during the spring to fall period. It follows, therefore, that the fall testes of this sexual class would weigh more since, as was shown in Text-figure 1, a positive correlation exists between the body size and the testicular weight of bears. There is a suggestion, nonetheless, that the seminiferous tubules of the infantile bear undergo slight shrinkage during the postbreeding season as in the mature animal (Table IV).

In contrast to both the infantile and adult bear, the testes of prepuberal bears remain essentially constant in weight from spring to fall (Text-fig. 2). This is presumably due to slight shrinkage of the seminiferous tubules following the breeding season in the spring, but this is accompanied by some compensatory growth of the body as a whole (Table III and compare Pl. III, fig. 12 and Pl. IV, fig. 19).

Gross Features of the Male Reproductive Tract

Grossly the reproductive tract of the male brown bear differs only in relative size from that described for the black bear (Erickson and Nellor, '64). The species has a well-developed os penis which measures up to eight and one-half inches in length in older bears and, as in the black bear, the penis is capable of extrusion from its sheath only with the attainment of sexual maturity. The testes are scrotal from infancy and are held closely to the body except in the adult animal during the breeding season. They are then further removed from the body due apparently to relaxation of the scrotum and their enlargement through vascular engorgement and tubule hypertrophy (Table IV, and Pl. I, figs. 1 and 2). Concomitant with the attainment of sexual maturity the tip of the scrotum becomes bare and very darkly pigmented. The hair-free patch is reduced in size and less obvious in late fall animals due principally to scrotal shrinkage. However, once sexual maturity is attained complete refurring of the patch apparently does not occur since it was observed in bears killed from April through November. This character is thus a useful one for identifying sexually mature bears.

TABLE IV

TESTIS TUBULE AND EPIDIDYMAL DUCT MEASUREMENTS OF BROWN BEARS AS RELATED TO AGE AND SEASON [a]

Season	*Reproductive Status*					
	Infantile		Prepuberal		Mature	
	No. Spec.	Ave. Diam. (u)	No. Spec.	Ave. Diam. (u)	No. Spec.	Ave. Diam. (u)
Spring (Apr. 2-May 29)						
Tubule Diam.	4	97	5	159	31	245
Epididymal Duct Diam.	5	163	4	218	34	293
Summer (June 12-Aug. 3)						
Tubule Diam.	1	83	—	—	6	238
Epididymal Duct Diam.	—	—	—	—	5	254
Fall (Sept. 1-Nov. 11)						
Tubule Diam.	11	94	4	145	3	184
Epididymal Duct Diam.	11	180	4	199	3	237

[a] Includes only specimens whose tissue condition warranted measurements; average of five epididymal and 10 tubule measurements.

The testis of the brown bear is roughly ovoid in shape and is slightly compressed laterally (Pl. I, figs. 1 and 2). The organ is not particularly large for the animal's size. In the adult bear at the height of the breeding season it measures approximately 9 x 6 x 5 cm and weighs slightly over 80 gms. Three bears, 1821, 1827, and 1831 had body weights of 705, 630, and 560 pounds and testis weights, respectively, of 84, 78, and 52 gms. The epididymis of the bear is large and tightly attached to the dorso-lateral surface of the testis, as is the vas deferens which courses back along the epididymis (Pl. I, figs. 1 and 2).

The gross internal architecture of the testis is shown in Plate I, figure 3. The fibrous tunica albuginea is very heavy. The blood vessels of the tunica vascularis hypertrophy markedly during the breeding season and supply the major blood needs of the testis. The vascularis layer is most pronounced at the cephalic end of the gland, becoming diminished caudally as vascular elements are passed into the testis (Pl. I, fig. 3).

At the cephalic end of the testis portions of the tunica albuginea pass into the gland as the mediastinum testis, which consists of a core of fibrous connective tissue, minor blood vessels, and the rete testis. The mediastinum testis is central in position and extends approximately three-fourths of the length of the testis (Pl. I, fig. 3). This is continuous with finer laminae of connective tissue, the septulae testis which extend radially into the testis encompassing the individual lobuli testis, the germinative, and endocrine portions of the gland. The coiled seminiferous tubules connect with short, straight tubuli recti which convey the sperm from the apex of the lobules to a series of irregular spaces lined with low cuboidal epithelium, the rete testis, which extends throughout the mediastinum (Pl. IX, fig. 51).

The Histology of the Male Reproductive Tract

Infantile bear.—The seminiferous tubules of the infantile bear are simple, undifferentiated cords widely dispersed in a cellular connective tissue. There is little apparent change in their appearance in most bears until the animals reach two years of age (Pl. II, figs. 4 and 5). The seminiferous tubules then show marked enlargement and come to occupy a major portion of the testis mass (Pl. II, fig. 6). The tubules of the two-year-old bear at the time of the breeding season in May measure slightly less than 100μ in diameter, are lumenless and filled with an amorphous material of uncertain origin—possibly Sertoli cell cytoplasm. The epithelial membrane of the tubules is two to four cells thick and for the most part the cells resemble Sertoli cells with prominent nucleoli (Pl. II, fig. 6). However, certain cells are hypertrophied and show mitosis indicating that some among them are germ cells. These do not develop beyond spermatocyte stages, however, and they either degenerate in situ or are passed to the tubule center, become pyknotic, and disintegrate. Relatively few of these immature cell forms are passed to the epididymis and the vas deferens (Pl. II, figs. 7 to 9).

The interstitial cells of the two-year-old bear are abundant but the tissue occupies a minor portion of the testis. The cells contain relatively little cytoplasm, are crowded closely together, and the nuclei stain darkly (Pl. II, fig. 6). It is noteworthy, nonetheless, that bears of this age class apparently produce abundant androgen as indicated by the well-developed epididymis and vas deferens (Pl. II, figs. 7 to 9). These organs appear fully functional, the epithelium being pseudostratified columnar with stereo-cilia as in the typical sexually mature mammal. With rare exceptions, however, the epididymal ducts and the vasa deferentia are empty of spermatogenic elements during the spring breeding season (Pl. II, fig. 7). On the other hand, abundant secretion products and an amorphous coagulum are constant in these organs at all seasons (Pl. II, figs. 8 and 9).

Following the breeding season in spring, the reproductive tract of the two-year-old infantile bear shows slight retrogressive changes. By October the seminiferous tubules undergo some shrinkage. This is indicated by thickening and wrinkling of the basement membranes, and an increased density of the central cytoplasmic complex (Pl. III, fig. 10). There is also a decline in the cell population of the seminiferous tubules and an accompanying increase in pyknotic shed elements, although this was highly variable between bears. As in the spring infantile bear, most of the cells lining the basement membrane are Sertoli-like (Pl. III, fig. 10).

The intertublar tissue in the two-year-old fall infantile bear was more apparent than during the spring, was frequently arranged in strands, and the cytoplasmic-nuclear ratio of the Leydig cells was slightly greater (compare Pl. II, fig. 6 and Pl. III, fig. 10). In general, however, the histology of the testis of the two-year-old bear does not differ appreciably from spring to fall.

The same statement cannot be made for the epididymis and the vas deferens. By November these organs undergo marked retrogression from their highly active state during the spring (compare Pl. II, fig. 7 and Pl. III, fig. 11). By late fall the ducts become reduced in size, lose their cilia, and develop a thick, dense, connective tis-

sue coat. While most of the ducts are empty, a few contain abnormal and immature sperm cell elements, and a heavy coagulum is a common feature (Pl. III, fig. 11).

Prepuberal bear.—Unfortunately no prepuberal bears were obtained prior to the breeding season in May. However from this time on there was a marked increase in the size of the seminiferous tubules to approximately 160μ (Table IV) and the development of large, distinct tubule lumina (Pl. III, fig. 12). The interstitial tissue at this time appeared sparse and compressed between the swollen tubules. The Leydig cells seemed to have a slightly greater cytoplasmic-nuclear ratio than in the infantile spring bear (compare Pl. II, fig. 6 and Pl. III, fig. 14).

While the germinal epithelium of the spring prepuberal bear was only four or five cells thick, there was a considerable amount of spermatogenic activity and spermatogenic stages were quite readily differentiated from Sertoil cells (Table I, Pl. III, fig. 13 and Pl. V, fig. 24). Interestingly, however, spermatogenesis became arrested in the secondary spermatocyte and spermatid stages and, as in the infantile bear, the majority of these cells appeared to disintegrate in situ. A fair proportion were shed to the tubule lumine, however, and passed to the epididymis and vas deferens (Pl. III, fig. 15 to Pl. IV, fig. 17). In this process multinucleate giant cells were often formed (Pl. III, figs. 13 and 15), apparently by a coalescence of developing germ cells in situ or a failure of the cell clones to separate (Fawcett, 1961). These are thought to indicate an animal in less than full reproductive vigor (Parks, '60).

As with the two-and-one-half-year infantile bear, the epididymis and vas deferens of the spring prepuberal bear is well developed with abundant secretory products (Pl. IV, figs. 16 and 17). The diameters of the ducts are increased, however, over those of the infantile animal (Table IV). A notable difference from the infantile bear is the regular occurrence of immature and abnormal cell forms within the ducts (Pl. III, fig. 15). Relatively few of these reach the vas deferens which suggests that their degradation is continuous as they proceed down the tract (Pl. IV, figs. 16 and 17).

Following the breeding season the seminiferous tubules of the prepuberal bear show a loss of turgor and activity (Pl. IV, fig. 18). The tubules become reduced in diameter (Table IV), the basement membranes thicken and wrinkle, and the tubule lumina are markedly reduced (Pl. IV, figs. 19 and 20). This is accompanied by a reduction in the germinal epithelium to the point that Sertoli cells predominate over germ cells. Nevertheless spermatogenesis continues at a diminished rate, the formed elements continuing to degenerate either in situ or in passage to the tubule lumina and epididymal ducts.

Ultimately, during late fall, defoliation of the spermatogenic epithelium becomes so pronounced that the only cells remaining within the tubules appear to be Sertoli cells (Pl. IV, figs. 19 and 20). During spermatogenic decline, as during other stages of the cycle, not all bears or even all tubules of a given bear were in the same reproductive state (Pl. IV, figs. 18 and 20). These differences were not attributable to the "spermatogenic wave" phenomena.

During the declining phase of spermatogenesis in the prepuberal bear the interstitial tissue is strandlike, shows an apparent increase in cytoplasmic amount, and the Leydig cell nuclei are smaller and darker stained (compare Pl. III, fig. 14 with Pl. IV, figs. 19 and 20). This is accompanied by atrophy of the vas deferens and of the epididymis (Pl. IV, fig. 21 to Pl. V, fig. 24). The vas deferens is the first of these organs to undergo degenerative changes (Pl. V, figs. 23 and 24). Its decline precedes even that of the seminiferous tubules (compare Pl. IV, fig. 19 and Pl. V, fig. 24).

The first indication of retrogression of the vas deferens and epididymis is disorganization of the duct epithelia (Pl. V, fig. 23). This process becomes marked and is accompanied by a decrease in the size of the ducts (Table IV). By November the epithelium of the vas deferens is reduced to a layer of very low columnar cells, the primary duct contents being degradation products of the earlier pseudostratified epithelium, a few abnormal germinal elements, and coagulum (Pl. V, fig. 24). By contrast, the epididymis retains a functional appearance for at least an additional month (Pl. IV, fig. 21 and Pl. V, fig. 22) and in none of the prepuberal specimens available to us did the epididymis attain a state of involution similar to that shown by the vas deferens (Pl. V, fig. 24). Conceivably, however, such a state would have been seen if we had had specimens of this group extending beyond early November. A notable feature during the declining phase was a marked increase in the coagulum found within the ducts (Pl. IV, fig. 21 and Pl. V, fig. 22).

The Sexually Mature Bear

Redevelopment phase.—The earliest mature spring bear, 41 M, was taken April 2, 1963 (Table III). The activity state of this animal was, however, well advanced over a number of other specimens taken at later dates. Of particular interest among these was specimen 22 M taken April 22, 1962. The small size of this animal's skull, and its delayed spermatogenic

state as compared with a majority of the other mature specimens we examined, suggest that it was just attaining sexual maturity (Table III and Pl. V, figs. 25 and 26). Among the obviously sexually mature bears included in our collection, specimen 42 M taken April 18, 1963, exhibited the least advanced stage of spermatogenic development (Pl. V, fig. 27). The seminiferous tubules of this specimen appeared quite uniformly rounded and the surrounding intertubular tissue was stringy and loose. This suggests that the tubules were not as markedly swollen as later in the cycle. In general appearance the tubules were quite dense, and without a distinct lumen. They were densely packed with developing spermatocytes and spermatids (Pl. VI, fig. 28). A few tubules were, however, in a more advanced state and exhibited all stages of spermatogenesis including mature spermatozoa (Pl. VI, fig. 29).

In the redeveloping bear testis abnormal cell forms were frequently observed, particularly multinucleated giant cells (Pl. VI, fig. 30). The high frequency of abnormal and immature germinal elements seen in the epididymides and vasa deferentia of the late redeveloping bears suggests that the first germinal elements passed are largely nonviable forms (Pl. V, fig. 26, Pl. VI, figs. 29 and 33). A heavy coagulum was also regularly noted in the lumina of the redeveloping tubules (Pl. V, fig. 27, Pl. VI, figs. 28 and 30). This was probably in part Sertoli cell cytoplasm together with degradation products of abortive germinal elements phagocytosed by Sertoli cells (Vilar, '65).

The interstitial tissue of the redeveloping bear testis is abundant. The cells have a relatively large cytoplasmic-nuclear ratio and the abundance of large vacuoles in their cytoplasm is striking (Pl. VI, figs. 28 and 29).

While specimens of bear epididymides and vasa deferentia were not available from bears prior to late testicular redevelopment, the well-developed state of these organs from the earliest specimens available suggested that they became fully functional before the testes produced sufficient mature spermatozoa for fertile breeding (Pl. VI, figs. 31 and 32). And, as indicated earlier, immature and abnormal cell forms were regularly to be noted in the duct contents of the redeveloping bear epididymis and vas deferens. A further interesting character was a heavy and marked vacuolation of the epithelia of the epididymis and vas deferens. This is possibly a precursor of the abundant secretion products noted in these organs (Pl. VI, fig. 32).

Fully active animals.—As has been mentioned earlier, bears vary markedly in the time of attainment of full breeding condition. Apparently, however, all mature specimens are reproductively capable in May (Table III).

At the height of breeding capability the seminiferous tubules are much swollen and compressed together and thus appear flattened or polygonal in cross section (Pl. VII, fig. 34). The tubules have distinct lumina and all stages of spermatogenesis are to be seen in the germinal epithelium. Abnormal sperm are rarely noticed. While tufts of maturing spermatozoa are abundantly embedded in the cytoplasm of Sertoli cells, free sperm are seldom noticed in the tubule lumina which suggests their rapid transport to the epididymis (Pl VII, fig. 34). The tubule lumina are also free of the amorphous coagulum which was commonly noted in the redeveloping bear.

At the height of the breeding season the intertubular interstitial tissue of the mature bear appears sparse and dense (Pl. VII, fig. 34). The large, abundant cytoplasmic vacuoles noted in the interstitial tissue of the redeveloping bear are generally not noticed at this time except in the abundant interstitial tissue which invades the tunica albuginea and septulae testis (Pl. VII, figs. 38 and 39).

The epididymis and vas deferens of the brown bear at the height of the breeding season are greatly distended with sperm (Pl. VII, figs. 35 and 36). That the vas deferens, as well as the epididymis, is an important organ for sperm storage in this species is indicated by the fact that it becomes so distended with spermatozoa that the usual pseudostratified columnar epithelium becomes low columnar (Pl. VII, fig. 36). At the height of the breeding season abnormal or immature cell forms occur only rarely in the ducts, and the epithelium of the epididymis and vas deferens are largely devoid of the heavy vacuolations noted in the prepuberal and in the preseasonal mature bear (Pl. VII, figs. 35 and 36). Bleb-like secretions are frequently to be seen however at the tips of the stereocilia (Pl. IV, fig. 6). The source of these is presumed to be the abundant vacuoles noted in the epithelia of the vasa deferentia and epididymides of the seasonal adult and prepuberal bear, and they are further the apparent source of the abundant secretions noted among the stereocilia in these animals (Pl. IV, fig. 17 and Pl. VI, fig. 32). It would appear, therefore, that there is a build-up of secretion products during the nonbreeding period and that the release of these products exceeds their build-up during the breeding season.

Postseasonal animal.—Following the limited breeding season in the spring, the male brown

bear shows spermatogenic decline. The time of the decline varies widely between bears (Pl. VII, figs. 37 and 39). The first sign of seminiferous tubule atrophy is the appearance of considerable numbers of abnormal and immature cell forms (Pl. VII, figs. 37 and 38). Spermatogenesis continues but is arrested in the secondary spermatocyte and spermatid stages. This condition closely parallels spermatogenesis as it occurs in the prepuberal and the preseasonal mature bear, particularly as regards the formation of multinucleated giant cells (Pl. III, fig. 13; Pl. IV, fig. 18 and Pl. VI, fig. 30). During the early phases of decline the germinal epithelium becomes reduced to four or five cells in thickness and tubule lumina become more distinct (Pl. VII, fig. 39 and Pl. VIII, fig. 40). This is followed by tubule shrinkage as manifested by a reduction of the luminar and a thickening and folding of the basement membranes (Pl. VII, fig. 38 and Pl. VIII, fig. 42). Defoliation of the spermatogenic epithelium continues until ultimately many, if not most, of the tubules are reduced to simple cords, the sole cell population of which consists of a single layer of cells lining the basement membrane as in senile testes (Pl. VIII, figs. 41 to 43). As in the prepuberal bear during the postbreeding season, these cells appear to be Sertoli cells.

Since we had no specimens extending beyond November, it was not possible to determine how complete seminiferous tubule decline becomes. The indications are, however, that the condition becomes quite general at the height of decline, presumably in midwinter when the animals are in their winter dens.

The interstitial tissue of the mature bear testis during the late postbreeding period appears slightly more abundant than during the breeding season. There is an apparent increase in the amount of cytoplasm within the cells but the vacuoles do not appear to attain the size of those seen during the prebreeding season (compare Pl. VI, figs. 28 and 29 and Pl. VIII, figs. 40 to 42). The interstitial tissue at this time is strand-like, the nuclei being dense and dark staining, and intercellular spaces are common. While these spaces were perhaps in part artifacts, we believe they represent decreases in cell size possibly coupled with edema. Concomitant with seminiferous tubule atrophy during the postbreeding season in the adult bear there is an accompanying but slightly later decline of the vas deferens and the epididymis (Pl. VIII, fig. 44 to Pl. IX, fig. 49). This is suggested by the appearance of immature and abnormal cell forms in the ducts before any discernible change in the histology of these organs. The passage of aberrant forms continues and ultimately they prodominate over normal forms in the duct contents (Pl. VIII, fig. 45). This is accompanied also by a marked reduction in the sperm load. In some instances the epididymal ducts are largely empty of germinal elements before there is any recognizable gross change in the epididymis itself (Pl. IX, fig. 46). In other cases some disorganization of the epithelium lining the epididymal ducts becomes obvious while germinal elements are still evident. Surprisingly, however, the vas deferens declines well in advance of the epididymis (compare Pl. VIII, fig. 45 and Pl. IX, fig. 48), the epithelium becoming low cuboidal and the duct contents consisting solely of degradation products and degenerate sperm (Pl. IX, fig. 48). In certain specimens such a condition occurred as early as September while in others a fairly healthy condition existed as late as November (Table III).

The limited number of fall specimens available to us did not afford a complete picture of epididymal decline in the adult bear. It appears likely that at the height of decline the epithelium of the epididymis roughly resembles that attained by the vas deferens. It is certain that during this time there is a marked reduction in the diameter of the epididymal ducts together with a relative increase in the connective tissue surrounding them (Table IV and Pl. IX, fig. 49).

Sperm morphology.—Mature brown bear spermatozoa appear typically mammalian in form with an overall length of 78.2μ. The head of the sperm is round to oblong in greatest length-width aspect, and flattened with a slight inflection of the head tip. The length and width of the head are 7.4 and 4 μ respectively. The cylindrical midpiece measures 11.5 μ and in sperm taken from the epididymis it typically retains a midpiece cytoplasmic droplet (Pl. IX, fig. 50). The attachment of the midpiece to the head is slightly abaxial. The length of the tail is 57.0 μ and the length of the terminal fibrilis 2.3 μ. These measurements fall within the range of values reported for other mammalian species (Parkes, '60).

Discussion

Although criteria for estimating the ages of brown bears have not been developed, several characters discussed in this study appear to have merit as indices for estimating the reproductive status and age of the male bear. The histology of the testis, regardless of the season, appears definitive for establishing the sexual status of bears as being infantile, prepuberal, or sexually mature. While a more extensive collection of known-age specimens is necessary to determine more closely the ages represented by each sexual group, these preliminary data suggest that the infantile class is represented by bears less than

three years of age and the sexually mature class by bears four years and older. The prepuberal class is mostly bears in their third year of life, although a few two-year and four-year animals are believed to be included also.

The weight of the testis and the size of the skull appear equally useful as indices of the age and sexual status of male bears. As judged from the histology of the testis, infantile bears generally have single testis weights of less than 25 gms and skulls measuring less than 22 inches in length plus width. Conversely, the single testis weights of sexually mature bears ranged upward from approximately 50 gms and the skulls seldom measured less than 24½ inches in length plus width. The testes and skulls of prepuberal animals lie roughly between those of the infantile and sexually mature groups with some slight overlap with both as was also true for the histological classifications. Nonetheless, skull sizes and testicular weights, particularly if taken together, appear to be fairly reliable criteria for classifying bears as to sexual status and relative age (Text-fig. 1). Other criteria described as useful for identifying the sexually mature bear were: capacity of the penis to be manually extruded from its sheath, and the presence of a darkly pigmented hairless patch at the tip of the scrotum.

These studies show that the male brown bear is a seasonal breeder. the reproductive period beginning before and extending beyond the breeding season of the female. As contrasted with the more limited and consistent reproductive period of the female, that of the male appears to last four or five months and varies markedly between individual bears. Certain specimens are in full reproductive vigor well in advance of the time of peak breeding while others appear reproductively capable until near the time of denning in November.

It seems, therefore, that the male brown bear has a potential breeding season slightly exceeding half of the year and encompassing the greater portion of the den-free period. The differing testicular histology throughout this period suggests, however, that individual bears are sexually capable for perhaps only about half of the potential breeding period (Table I). It is significant that during the period of normal female reproductive activity from late May to early July (Dittrich and Kronberger, '63) practically all sexually mature bears are producing abundant spermatozoa (Table III).

From a comparative point of view, certain aspects of the morphology and histology of the brown bear reproductive tract are extremely interesting. The high development of the epididymis and the vas deferens of the immature one-and-two-year old bear well in advance of any spermatogenic activity was remarkable and was seemingly typical of the state attained by the sexually mature animal. To our knowledge such an advanced state of development at least two years in advance of the attainment of sexual maturity is unique among mammals studied to date with the exception of the closely related black bear (Erickson and Nellor, '64). The high degree of spermatogenic activity attained by the prepuberal bear a full year in advance of sexual maturity was similarly striking.

Perhaps the most interesting feature of the histology of the male bear's reproductive tract is the marked atrophic state exhibited by the testis in the nonbreeding season. While the specimens available to us did not permit a determination as to how general the atrophic state becomes, the indications were that the senile appearance of the seminiferous tubules becomes quite general at the height of decline, presumably in midwinter when the animals are in winter dens. This was suggested both by the almost complete atrophy of the tubules during the nonbreeding season in the seasonally quite active prepuberal bear (Pl. IV, figs. 18 and 19), and by the large proportion of senile tubules in the late declining adult bear (Pl. VIII, figs. 42-44).

In light of this it appears warranted to speculate as to the manner in which the germinal epithelium becomes repopulated; whether it be from a far advanced or more limited state of atrophy. Three explanations may be advanced. First it may be that the Sertoli-like cells remaining in the tubules are really a mixture of spermatogenic and Sertoli cells but are not recognizably different. A second postulate is that the cells are truly a single cell type but bipotential. The third possibility is that portions of the tubules fail to undergo the marked atrophy indicated in Pl. VIII, figs. 41 to 43 and these residual centers repopulate the tubules. Of these possibilities the latter appears the most plausible for the following reasons: As indicated in Pl. VIII, figs. 41 and 43, wide variations were seen between the condition of tubules not only between bears but even within a given testis. Even in animals showing a high percentage of senile-type tubules, other tubules could be found showing active spermatogenesis. It was interesting too that seminiferous tubule decline appeared in some cases to be affecting only individual tubules (Pl. VIII, fig. 41), but in other cases whole lobuli testes (Pl. VIII, fig. 43). This is taken as evidence that atrophy begins at given points within the tubules and then spreads progressively along their length.

We believe that seminiferous epithelial repop-

ulation (postulate 1) cannot be explained as resulting from a mixture of cells in which spermatogonia and Sertoli cells are indistinguishable. The irregularly spherical shape of the nucleus and the large, dark-staining, eccentrically located nucleolus is typical of Sertoli cells. None of these nuclei showed a condition suggestive of meiosis which further reduces the possibility of their being spermatogonia, and therefore also lowers the probability that they are bipotential as suggested by postulate two.

Another interesting feature of the histology of the brown bear testis is the marked degree to which the interstitial tissue invades the tunica albuginea (Pl. VII, fig. 39). Furthermore, the Leydig cells in these areas have a relatively large cytoplasmic-nuclear ratio, in which their large vacuoles are an important factor. Then too, while the intertubular interstitial tissue of the fully active animal appears to possess a much lower cytoplasmic content than at other times in the cycle, the cells in the tunic consistently maintained their seemingly high functional state.

The secretion products of the epididymides and vasa deferentia are apparently proliferated from their highly active stereo-ciliated epithelial cells, and vary in amount between bears. In the prepuberal bear at all seasons, and in the preseasonal and early postseasonal sexually mature bear, the basal cells of the epithelia of these organs commonly contain large numbers of vacuoles (Pl. VI, fig. 32). A similar state is rarely seen in the fully active animal. Rather the vacuoles appear at this time to have migrated toward the apical ends of the cells and the frequently observed bleb-like formations among the stereocilia may be a product in some way related to them. This sequence suggests a build-up of these products during the nonbreeding season and a depletion (over build-up) during the active reproductive period.

The abundant coagulum throughout the tract is apparently of varied origin and again appears to be related to the reproductive state of the animal. It seems to be absent in the fully active adult, present in low amounts in the prepuberal animal, and quite abundant in the seasonal adult, particularly during the preseasonal period (Pl. IX, fig. 46.) While some of this material may conceivably be of Sertoli cell origin, the larger amount appears to be degradation products of degenerate sperm cells phagocytozed by Sertoli cells (Vilar, '65) and possibly by lymphocytes. Further degradation of degenerate sperm appears to occur in the epididymis and vas deferens and adds to the coagulum load in these organs. Additional coagulum is believed to be added to the ducts of the epididymis and the vas deferens by liquifaction of the secretions of these organs and by the addition of cytoplasmic material from maturing sperm.

An additional interesting observation in the declining bear is the frequent invasion of lymphocytes into and surrounding the seminiferous tubules, the epididymides, and deferent ducts. A similar condition frequently occurs in the prepuberal and preseasonal adult bear (Pl. IV, fig. 19 and Pl. VIII, fig. 45). While this condition would normally suggest a pathologic state, it is too general throughout our specimens to be attributed to this. A possible explanation is that the lymphocytes are involved in the breakdown of both the epithelial debris from the ducts and of the great numbers of degenerate germinal cells.

Literature Cited

Couturier, M. A. J.
1954. L'ours Brun. Grenable. 904 pp.

Dathe, H.
1961. Beobachtungen zur Fortpflanzungsbiologie des Braunbären, *Ursus arctos* L. Der Zool. Garten (NF), 25:235-250.

DeVoto, B. A.
1953. The journals of Lewis and Clark. Bernard DeVoto, Ed. Houghton Mifflin Co., Boston. 504 pp.

Dittrich, L., and I. V. Einsiedel
1961. Bemerkungen zur Fortflanzung und Jugendentwicklung des Braunbären (*Ursus arctos* L.) im Leipziger Zoo. Der. Zool. Garten (NF), 25:250-259.

Dittrich, L., and H. Kronberger
1963. Biologisch-anatomische Untersuchungen über die Fortpflanzungs-biologie des Braunbären (*Ursus arctos* L.) und anderer Ursiden in Gefangenschaft. Zeitschrift for Saugetierkunde, 28:129-192.

Erdbrink, D. P.
1953. A review of fossil and recent bears of the old world. Doct. Diss., Jan de Lange, Deventer. 597 pp.

Erickson, A. W., and J. E. Nellor
1964. Breeding biology of the black bear. *In:* The black bear in Michigan, Pt. I, Mich. Agr. Exp. Sta. Research Bull. No. 4, Mich. State Univ., East Lansing. 5-45.

Fawcett, D. W.
1951. Intercellular bridges. Exper. Cell Research, Supplement B:174-187.

Murie, A.
1944. The wolves of Mount McKinley. Fauna of the Natl. Parks of the U.S., Fauna Series No. 5. 238 pp.

Parks, A. S.

1960. Vol. I, Pt. II. Marshall's physiology of reproduction. A. S. Parks, Ed. Longmans, Green and Co. Ltd., Toronto. 877 pp.

Pocock, R. I.

1932. The black and brown bears of Europe and Asia. Pt. I, J. Bombay Nat. Hist. Soc., 35:771-823.

Rausch, R. L.

1962. Geographic variation in size in North American brown bears, *Ursus arctos* L., as indicated by condylobasal length. Canad. J. Zool., 41:33-45.

Troyer, W. A., R. J. Hensel, and K. E. Durley

1962. Live trapping and handling of brown bears. J. Wild. Mgt., 26:330-331.

Vilar, O.

1965. An electron microscopial study of the phagocytosis of germinal cells by Sertoli cells in tissue cultures. Anat. Record, 151: 428-429.

Wimsatt, W. A.

1963. Delayed implantation in the ursidae, with particular reference to the black bear (*Ursus americanus* Pallas). *In:* Delayed Implantation, Univ. Chicago Press, Chicago. 49-76.

EXPLANATION OF THE PLATES

Plate I

Figs. 1 & 2. Whole testis of a fully active bear showing well-developed epididymis and vas deferens. E-305, 5/11, X2/5.

Fig. 3. Internal architecture of the active testis. E-305, 5/11, X9/16.

Plate II

Fig. 4. Testis of a one and one-half-year infantile bear during the breeding season. Seminiferous tubules are undifferentiated cords widely dispersed in loose cellular connective tissue. 65M, 5/21, X27.

Fig. 5. Testis of a one and one-half-year infantile bear during the postbreeding season. Seminiferous tubules occupy a greater portion of the mass of the testis than in Plate II, figure 4, and the intertubular tissue shows slightly greater interstitial cell abundance. 46N, 1-½, X34.

Fig. 6. Testis of a two and one-half-year infantile bear during the breeding season. Seminiferous tubules are enlarged, lumenless, and occupy a major portion of the testis. Epithelial lining is two to four cells thick. The nuclei of most of these cells resemble Sertoli cell nuclei; however, a few cells hypertrophy and undergo cell division but degenerate. Interstitial cells are relatively abundant but contain little cytoplasm and, consequently, occupy a minor portion of the testis. 12M, 5/7, X67.

Fig. 7. Well-developed epididymis of the two- and one-half-year bear during the breeding season. The ducts are characteristically free of germinal elements. 12M, 5/7, X67.

Fig. 8. Abundant secretion products are common in the nondegenerate epididymis of the two-year infantile and prepuberal bear, and in the preseasonal and early postseasonal adult bear. 18M, 10/31, X107.

Fig. 9. Amorphous coagulum is common in the nondegenerate vas deferens of the two-year infantile and prepuberal bear, and in the preseasonal and early postseasonal mature bear. The presumed origin of the material is liquefaction of secretion products and the breakdown products of degenerate germinal elements. 12M, 5/7, X67.

Plate III

Fig. 10. Testis of a two and one-half-year infantile bear during the postbreeding period. Seminiferous tubules are shrunken, basement membranes thickened and wrinkled, and the density of the central cytoplasmic complex increased. Interstitial tissue is relatively more abundant than during the breeding season with an increased cytoplasmic-nuclear ratio. Cf. Plate II, figure 8. 47N, 10/22, X32.

Fig. 11. Postseasonal retrogression of the two and one-half-year infantile epididymis. Epididymis is nonfunctional, stereocilia are lost, and ducts reduced in size and surrounded by a thick, fibrous connective tissue coat. Most ducts are empty except for a heavy coagulum. Cf. Plate II, figure 9. 52N, 10/29, X30.

Fig. 12. Testis of the prepuberal bear during the breeding season. Seminiferous tubules are markedly swollen and have a large lumen. Interstitial cells are sparse, confined to interstices between the tubules, and have a slightly higher cytoplasmic-nuclear ratio than in the spring infantile bear. 21M, 5/22, X27.

Fig. 13. High power showing spermatogenic activity becoming arrested in the spermatocyte and spermatid stages in the prepuberal bear. The formation of multi-nucleated giant cells is a common feature. 21M, 5/22, X67.

Fig. 14. High power showing greater cytoplasmic-nuclear ratio of the interstitial tissue of the spring prepuberal bear as compared to the infantile bear. Cf. Plate II, figures 2 and 3. 21M, 5/22, X67.

Fig. 15. Immature and abnormal germ elements shed to the epididymis of the spring prepuberal bear. Most of the cells disintegrate in situ relatively few being passed to the epididymis and even fewer to the vas deferens. 21M, 5/22, X67.

PLATE IV

FIG. 16. Prepuberal vas deferens showing limited numbers of immature and abnormal germ cells and the bleb-like secretions at the tips of the stereocilia. 21M, 5/22, X38.

FIG. 17. Vas deferens of the prepuberal bear showing degenerate germ elements, including several spermheads, and highly active stereo-ciliated cells with abundant basally located presumed steroid products. 59M, 5/11, X67.

FIG. 18. Declining spermatogenic activity in the postseasonal prepuberal bear. The tubules are reduced in diameter, the basement membranes thickened and wrinkled, and the germinal epithelium and lumina reduced. Note the occurrence of lymophocytes in the upper right tubule. 62A, 10/4, X67.

FIG. 19. Continued testicular decline in the fall prepuberal bear. The lumina of the seminiferous tubules are reduced markedly and Sertoli cells predominate over the germinal forms. Interstitial tissue is more prominent than in the spring bear (Plate III, fig. 13). The cells are arranged in strands and have an increased cytoplasmic-nuclear ratio. Note the accumulation of lymphocytes at the lower margin of the upper left tubule. 73M, 10/14, X67.

FIG. 20. Seminiferous tubules showing complete loss of spermatogenic elements in the postseasonal prepuberal bear. Note also the difference in activity state between various tubules within a given testis (Pl. IV, fig. 18). 62A, 10/4, X67.

FIG. 21. Declining epididymis in the fall prepuberal bear. Epididymal ducts are becoming reduced in diameter and are being enveloped by a thick, fibrous, connective tissue coat. 62A, 10/4, X27.

PLATE V

FIG. 22. Epididymis of the late fall prepuberal bear retaining a functional state beyond that of the vas deferens (Pl. V, fig. 23). Note the coagulum in the ducts. 9M, 10/10, X67.

FIG. 23. Declining vas deferens in the late fall prepuberal bear. The decline precedes that of the epididymis (Pl. V, fig. 22) and is marked by a reduced duct diameter, and disorganization of the epithelium. 9M, 10/10, X30.

FIG. 24. The prepuberal vas deferens in late decline. Duct epithelium is reduced to a single layer of low cuboidal cells. The duct contents are degradation products and a few abnormal cells. The ducts are surrounded by a thick, fibrous, connective tissue coat. Note that the decline of this organ precedes that of the seminiferous tubules (Pl. IV, fig. 19). 73M, 10/14, X38.

FIG. 25. A presumed first-year adult showing spermatogenic activity in excess of that noted for the prepuberal bear (Pl. III, fig. 13) and with more abundant interstitial tissue. 22M, 4/22, X67.

FIG. 26. Epididymis of presumed first-year adult showing a relatively large number of germinal elements, including a number of sperm heads. This condition parallels that of the fully mature bear at the approach of the breeding season when abnormal forms predominate. 22M, 4/22, X74.

FIG. 27. Spermatogenic activity in the adult bear early in the breeding season. The tubules are rounded without distinct tubule lining and are not markedly swollen as they are later in the season. 42M, 4/18, X34.

Plate VI

Figs. 28 & 29. Differing states of spermatogenesis between tubules. Interstitial tissue is abundant, loose, and stringy with a high cytoplasmic-nuclear ratio. The large size of the vacuoles within the cytoplasm is remarkable. 42M, 4/18, X67.

Fig. 30. Multinucleated giant cells commonly observed in the redeveloping and declining adult testis, and in the prepuberal and two-year infantile testis. 6M, 5/15, X67.

Fig. 31. Well-developed state of the epididymis of the early redeveloping bear. The sperm load is light and abnormal forms are common. 42M, 4/18, X67.

Fig. 32. Redeveloping bear epididymis. Abundant accumulations of material among the stereocilia is a common feature. 1M, 5/4, X67.

Fig. 33. Vas deferens of the redeveloping bear showing early sperm load containing large numbers of immature and abnormal germinal elements. 42M, 4/18, X42.

Plate VII

Fig. 34. Testis of the fully active animal. The seminiferous tubules are markedly swollen and compressed together, with distinct lumina and all stages of spermatogenesis. Abnormal elements are rare. Interstitial cells are sparse and exhibit a relatively low cytoplasmic-nuclear ratio. 27M, 5/20, X54.

Fig. 35. Epididymis at the height of the breeding season containing a heavy sperm load practically free of immature and abnormal forms. 1396, 5/12, X67.

Fig. 36. Vas deferens at the height of the breeding season. The heavy sperm load suggests that the vas deferens is an important organ for sperm storage in this species. 17M, 5/23, X67.

Fig. 37. Early spermatogenic decline in the adult bear. Spermatogenesis is becoming arrested in the spermatocyte and spermatid stages and abnormal forms are increasing. Interstitial cells are more abundant than during the breeding season and have larger amounts of cytoplasm (Pl. VII, fig. 34). However, the cytoplasmic-nuclear ratio is less than in the redeveloping testis (Pl. VI, figs. 28 and 29). 54N, 11/10, X89.

Fig. 38. Degeneration of the germinal epithelium in the declining adult bear is accompanied by tubule shrinkage, thickening of the basement membranes, and the appearance of intertubular spaces. 54N, 11/10, X67.

Fig. 39. Early declining testis showing reduction of the germinal epithelium and the peculiar and marked extension of the interstitial tissue into the tunica albuginea. 1820, 7/17, X27.

PLATE VIII

FIG. 40. Further defoliation of the spermatogenic epithelium of the declining bear. Note particularly the formation of multinucleated giant cells probably by the coalesence of developing germ cells. 1820, 7/17, X67.

FIG .41. Complete loss of spermatogenic elements in individual tubules of the declining bear. 1831, 7/21, X30.

FIG. 42. High magnification showing that the remaining cell population is Sertoli cells. 1831, 7/21, X67.

FIG. 43. Marked germ cell degeneration affecting a whole tubule while spermatogenesis is still evident in adjacent tubules. 1831, 7/21, X30.

FIG. 44. Apparently functional epididymis in a bear with marked spermatogenic decline (Pl. VII, fig. 37). The epididymal ducts are largely empty except for limited abnormal forms, secretory products, and coagulum. 54N, 11/10, X27.

FIG. 45. Epididymis of the declining bear. The germinal elements are largely abnormal, the duct diameter reduced, and the epithelium disorganized. Heavy lymphocyte invasion (left) is general. 55N, 11/10, X67.

PLATE IX

FIG. 46. Declining bear showing epididymis largely free of germinal elements but with abundant coagulum the source of which is liquefaction of secretion products and degenerate germinal cell forms. 54N, 11/10, X67.

FIG. 47. Vas deferens of the declining bear just prior to the major degenerative change (Pl. IX, fig. 48). 54N, 11/10, X34.

FIG. 48. Atrophic vas deferens in the postseasonal bear. The epithelium is reduced to a single layer of low cuboidal cells, and the ducts are markedly reduced and surrounded by a thick, dense, connective tissue coat. Duct contents are largely debris and a few abnormal germ cells. 55N, 11/10, X34.

FIG. 49. Epididymis of the late postseasonal bear. The ducts are reduced in diameter and surrounded by a heavy connective tissue coat. 55N, 11/10, X27.

FIG. 50. Brown bear epididymal sperm typically retain a midpiece cytoplasmic droplet. Sperm washed from 10 percent formalin-fixed testis tissue and postfixed in O_sO_4. Overall length of sperm is 78.2 μ. E-305, 5/11.

FIG. 51 A portion of the very profuse rete testis of the brown bear (Pl. I, fig. 3). The epithelium is typically a single layer of low cuboidal cells. 62A, 10/4, X84.